The Soil Reactions of certain Rock Ferns—II

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Asplenium ebenoides appears to have been found most frequently on limestone, although its type locality was on gneiss or schist, and at the famous occurrence at Havana, Alabama, the rock is described as a conglomerate. At several stations located by Messrs. Pretz and Young near Allentown, Pennsylvania, and Natural Bridge, Virginia, respectively, the rocks are limestone, and the soil reactions alkaline or, where the fern grows in moss coating the rocks, slightly acid. Near Harper's Ferry, West Virginia, a plant kindly shown to the writer by Dr. T. C. Stotler grows on shale, and the soil is minimacid. The soils in the pockets in schist rock, where this species has been found along the Potomac northwest of Washington, are likewise moderately acid. The soil on herbarium specimens collected by Mr. Maxon at Havana was found to have a high minimacid reaction. This fern is therefore inferred to be a calcareous soil plant, somewhat tolerant of acid conditions.

Asplenium platyneuron (*ebeneum*) grows with apparently equal frequence in both moderately acid and alkaline soils, the statement sometimes made that it prefers limestone coming apparently from the lack of appreciation of its abundance and luxuriance in many regions where there occur no limestone or other calcareous rocks whatever. It is interesting to note, however, that this fern tends to avoid soils of greater acidity than subacid, and when growing in regions of dominant mediacid soils, as in the Pine-Barrens of New Jersey, it is most often found on steep banks where soils of subacid reaction are developed. In southern Delaware it occurs in isolated patches in pine woods, and tests have shown the soils of these areas to be distinctly less acid than are those of the

region in general, due either to locally more complete decomposition of the vegetable matter, or to the presence of more or less calcareous lenses in the underlying sand formation. These facts, together with its occurrence on limestone rocks, lead to its classification as a calcareous soil plant tolerant of acidity to a considerable but not an extreme degree.

Asplenium resiliens (*parvulum*) has been recorded more often on limestone than on other rocks, and several observations upon it, in southern Virginia, confirm the correctness of its usual classification as a calcareous soil plant practically intolerant of acid conditions. It is usually rooted in limestone fragments of alkaline reaction, and even in occurrences in mossy humus the acidity was not observed to exceed low minimacid values. The more widespread *Asplenium Trichomanes,* observed throughout the region studied, is well known to occur on all sorts of rocks. On limestone it often grows in the open, in soil composed of rock fragments and accordingly alkaline in reaction. On sandstone, schist, gneiss, etc., it usually grows, however, in soils made up of decomposed vegetable matter accumulated in places more or less sheltered from the action of the rain, so that little lime can be leached out, and the reaction is circumneutral or rarely subacid. It is thus to be considered a calcareous soil plant moderately tolerant of acidity.

The writer has been unable to study *Asplenium viride* in the field, as his visit to the region of Willoughby Lake, Vermont, was too brief to permit a climb to its recorded place of growth near the top of the cliffs of Mt. Hor. The rock of this mountain is, however, a calcareous gneiss (of Ordovician age), so the fern would be suspected of calcareous soil tendencies. Tests of soils of specimens in the National Herbarium, from the locality at Smuggler's Notch, showed in fact neutral to very slightly acid reactions, confirming the correctness of this inference.

Most of the recorded occurrences of *Asplenium Bradleyi* are on sandstone, schist or gneiss rocks; there are only one or two references in the literature to its occurrence in limestone regions, and apparently none to its actual growth on limestone rocks. The statement in some manuals that it prefers limestone is thus clearly erroneous. It has been studied in the field only along the Susquehanna River in southern Pennsylvania, where the rock is schist and the soil reaction mediacid to subacid. Tests on herbarium specimens from Glen Onoko, Pennsylvania, Baltimore County, Maryland, and Whitfield County, Georgia, showed the same reactions. This species is therefore to be classed as an acid soil plant, but slightly tolerant of calcium. *Asplenium gravesii*, the hybrid between this and *A. pinnatifidum*, is stated to grow with the parents on sandstone rock, and is undoubtedly also partial to acid soils.

The relations of *Asplenium montanum* are practically identical with those of the preceding species. Reported almost exclusively on sandstone, schist, or gneiss and only in one or two doubtful instances on limestone, it would be suspected to be an acid soil plant; and the writer's tests upon it, at a number of localities in Pennsylvania, Virginia and West Virginia, have demonstrated the correctness of this conclusion. Its soil reactions are dominantly subacid, and it is relatively intolerant of calcium. The related *Asplenium Ruta-muraria* belongs, however, quite as definitely in the other class. The two or three reports of it on other rocks than limestone refer to shale, schist, and trap, on which calcareous soils often form. Observations made upon it, at several localities in Vermont, Pennsylvania, Maryland, and Virginia have shown it to be in fact practically limited to soils made up of limestone fragments; and it has not been found in material of more than the slightest degree of acidity, so it is classed as a calcareous soil plant prac-

tically intolerant of acid. The contrast between these two species will receive further attention later on.

Polypodium vulgare is difficult to characterize, as its habitats exhibit a wide range in both rock and soil character. It appears to be definitely limited however, on the acid side, failing to grow in mediacid soils; and, as it does grow in alkaline humus, even though infrequent on bare limestone rocks, it is classed as a calcareous soil plant rather tolerant of acidity. *Polypodium polypodioides* (*incanum*) belongs, however, to the other class. The reaction of the humus on tree trunks, in which it grows most frequently, is of course decidedly acid, often reaching the highest degree here considered. Subacid reaction is shown by the occurrence of this species on schist rock near Widewater, Maryland. It has been reported on limestone at several localities, but at the one available for study, in the gorge above Natural Bridge, Virginia, which is probably typical, its roots are embedded in thick moss coating the limestone ledges. The upper part of this moss, in which most of the fern roots lie, is distinctly acid in reaction, and only the layers nearest the rock have the acidity neutralized. As the spores of the fern must have fallen and started to grow in the acid portion of this moss, such occurrences are not an indication that it is other than an acid soil plant, at most somewhat tolerant of calcium.

Woodsia glabella is well known to occur on the cliffs of calcareous gneiss at Willoughby Lake, Vermont, and repeated tests made there showed circumneutral reactions throughout, the fern avoiding strictly the patches of subacid soils which occur here and there in that region. This fern has been reported, to be sure, in a few places where the rocks are not known to be calcareous, but most of its localities are definitely in limestone regions. The rarer *Woodsia alpina* (*hyperborea*) is found in the same localities but in more exposed situations,

where lime becomes more or less leached from its soils. These ferns are both classed as calcareous soil species, the latter the more tolerant of acidity.

Woodsia Ilvensis has been recorded most frequently on noncalcareous rocks, comprising sandstone, shale, schist and trap, and not a single mention of its occurrence on limestone could be found in the literature. One colony of it was observed at the extreme top of the Willoughby cliffs, so exposed as to be subjected to thorough leaching by the rain, and tests of the soil showed it to be somewhat acid, in spite of the calcareous nature of the adjacent gneiss rocks. In numerous occurrences of the same species in Pennsylvania, as well as one in West Virginia, the rocks are sandstone and shale, and the reactions are dominantly subacid. Although not found in the most acid soils, this species seems most correctly classified as an acid soil plant fairly tolerant of lime. The more abundant and widespread *Woodsia obtusa* grows on all sorts of rocks, but is best developed on limestone. When growing on schist and similar rocks its soil reactions have been found to be often subacid, so it is classed as a calcareous soil species rather tolerant of acidity.

Filix (*Cystopteris*) *bulbifera* grows, throughout the region covered, mostly in talus at the bases of cliffs of limestone as well as of various other rocks. Its soils are likely to contain considerable leafmold, and to be circumneutral in reaction, subacid reactions having been but rarely observed. It is evidently to be classed as a calcareous soil species, somewhat tolerant of acidity. The even more abundant *Filix* (*Cystopteris*) *fragilis* grows on ledges of sandstone, schist and shale, as well as of limestone rocks, and also in talus and in woods entirely apart from any rocks. Tests of its soils have given about the same results as with the preceding species, but as would be expected from its growth on the

rock types first mentioned, it is still more acid-tolerant. It avoids, however, mediacid soils.

Although there has been no opportunity to study *Dryopteris* (*Aspidium*) *fragrans* in the field, its relationships seemed of sufficient interest to make tests on herbarium specimens worth while. It has been recorded as growing on presumably noncalcareous slate or schist in several northern regions; but as appearing most commonly in localities where limestone rocks are dominant, although in exposed situations, where the lime might be leached out by the rain. The National Herbarium contains specimens with soil adherent to the roots from the cliffs of schist rocks at Smuggler's notch, and those of limestone conglomerate near Bic, Quebec. As anticipated, the soil reactions in both of these cases proved to be distinctly acid. The acidity is not, however, great enough to throw doubt on the correctness of its usual classification as a calcareous soil plant, if it is regarded, like several others belonging in this class, as rather tolerant of acidity.

Soil Reaction and Plant Relationship

Close relationship between plants, whether they be classed as separate genera, species, or varieties, implies derivation either from the same ancestor or from one another, by some process of natural selection, mutation, or hybridization. Studies of soil reaction, such as are described in the present paper, are of course not capable of deciding what source or what process were concerned in any given case; but when, as in certain of those above described, two related plants show a marked difference in soil preference or in tolerance to acid or to calcium, it is perhaps safe to infer that neither represents a present-day mutant or hybrid of the other.

In the case of the genus *Cheilanthes* the data are inadequate for discussion. Of the *Pellaeas*, however, one, *P.*

atropurpurea, is much more tolerant of acid conditions than the other. *Camptosorus rhizophyllus* and *Asplenium pinnatifidum*, which seem to the writer to be more closely related than the usual nomenclature would suggest, because of their convergence in such characters as structure of the cells in their stipes and scales, rooting at the frond-tips, and even netted arrangement of veins,[5] as well as the ability of the former to hybridize with at least one species of *Asplenium*—are even more strikingly different in soil preference. The former is a calcareous soil plant, somewhat tolerant of acidity; the latter, an acid soil plant, only slightly tolerant of calcium.

Asplenium Bradleyi is essentially identical in soil requirements with *A. montanum*, both being acid soil plants intolerant of calcium; but the relative of the latter, *A. Ruta-muraria*, differs radically in this respect, being an alkaline soil plant, almost intolerant of acidity. *Polypodium vulgare* and *P. polypodioides* also differ in their ultimate soil preference, although overlapping considerably in range of tolerance. *Woodsia glabella* is a calcareous soil species intolerant of much acidity, while the related *W. Ilvensis* is an acid soil plant not very tolerant of calcareous matter. It is interesting to note that *W. alpina*, which is intermediate between these in morphologic characters, is also intermediate in its preference to soil reaction. Finally, *Filix bulbifera* and *F. fragilis*, while alike in being calcareous soil plants, differ distinctly in tolerance for acid, the latter showing the greater.

Adaptation to contrasted soil reactions, with the physiological divergence it implies, seems to the writer likely to have required a long period of evolution. It is true that in a research frequently cited, Sadebeck[6] believed that he had produced a change of two *Aspleniums*

[5]Waters, C. E. Fern Bull., 10, 2, 1902.
[6]Ber. Sitz. Ges. Bot. Hamburg, 3, 4, 1887.

into related but physiologically distinct species in six generations. But some authorities on European ferns question the distinctness of the species concerned; moreover, it was possible to produce the alleged change in one direction only; and finally, the supposed physiological distinctness was not a matter of favoring acid on one hand and calcareous matter on the other, but tolerance to presumably high magnesium content of soil derived from serpentine rock, as contrasted with low magnesium content typified by ordinary garden soils.

In this connection it may be pointed out that in the case of *Asplenium ebenoides*, which is regarded by most authorities as a recent hybrid between *Camptosorus* and *Asplenium platyneuron*,—a view that has been confirmed experimentally—the hybrid does not deviate essentially in soil requirement or tolerance from its parents. The same is evidently true of *Asplenium gravesii*, also a present-day hybrid. It therefore appears that in the pairs or groups of related species above shown to exhibit contrasts in soil reaction, the greater the divergence in reaction, the longer time has been required for their development since the original separation. In the three most strongly marked cases, namely *Camptosorus* and *Asplenium pinnatifidum*, *Asplenium montanum* and *A. Ruta-muraria*, and the small *Woodsias*, it would be inferred that the separation occurred at some fairly remote geological time.

It may be urged, then, in concluding this paper, that in future discussions of relationships between such reaction-sensitive plants as these rock ferns it will be well worth while to pay some attention to the soil reactions.

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